

THE BREEDING BIOLOGY OF SMITH'S LONGSPUR¹

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SINCE 1930, when the railroad connecting the Canadian prairies with the port of Churchill, Manitoba, on Hudson Bay, was completed, the Churchill area has been the scene of many ornithological investigations. Despite this, many of the region's most interesting birds have remained virtually unstudied. One of these is Smith's Longspur (*Calcarius pictus*). Our present knowledge of this species on its breeding grounds (summarized by Kemsies, in Bent et al., 1968) is mainly from the preliminary accounts of Taverner and Sutton (1934) and Grinnell (1944). My studies at Churchill were primarily concerned with shorebirds, but as time permitted I gathered information on this beautiful and characteristic subarctic bird. Most of my observations were made in 1965 and 1966, but there was high nestling loss in 1965 (Jehl and Hussell, 1966a). Therefore, this paper emphasizes observations made in 1966, but supplementary data from 1964, 1965, and 1967 are included.

BREEDING RANGE AND HABITAT

The breeding range of Smith's Longspur extends from the Hudson Bay coast of Ontario westward, presumably along the treeline, into northeastern Alaska; a small population also breeds in northern British Columbia. The Alaskan and Ontario populations have been described as racially distinct from the central Canadian population but, for reasons discussed elsewhere (Jehl, 1968), the species must be considered monotypic.

At Churchill, and probably throughout its breeding range, this longspur is a bird of the forest-tundra—the more northerly part of the transition zone between the boreal forest and the treeless tundra (Johansen, 1963). Within this zone it occurs most frequently where the drier sedge meadows dominated by *Scirpus caespitosus* and dwarf birch (*Betula glandulosa*) are interrupted by low hillocks or small ridges (usually old beach lines) bearing scattered, isolated clumps of black spruce (*Picea mariana*), or, less frequently, larch (*Larix laricina*). The hillocks rise only a few feet above the surrounding area and are dominated by heaths, principally *Rhododendron lapponicum*, *Andromeda glaucophylla*, *Arctostaphylos* sp., *Vaccinium uliginosum*, and *Vaccinium vitis-idaea*; other common plants include *Dryas integrifolia*, *Empetrum nigrum*, *Salix reticulata*, and *Cladonia* spp. (Fig. 1).

The commonest nesting associates of Smith's Longspur in this habitat are

¹ This paper is dedicated to George Miksch Sutton in recognition of his pioneering ornithological research at Churchill, Manitoba, and elsewhere in the Canadian Arctic.

Savannah Sparrows (*Passerculus sandwichensis*), and Least (*Erolia minutilla*) and Stilt sandpipers (*Micropalama himantopus*).

ARRIVAL

A few male Smith's Longspurs appear at Churchill in late May, but their major influx occurs in the first week of June. Females arrive several days later. In 1965 and 1966 (Fig. 2), most males arrived by 6 June; single females were seen in the first days of June but the peak of arrival was from 7 to 9 June. Early June 1967 was relatively cool and males arrived through 11 June, though females did not appear until that date. Arrival in the exceptionally cold and wet spring of 1964 was even more retarded. A male was observed on 29 May, but the species was not encountered again until 15 June, when another male appeared. On 16 June large flocks of males and females arrived and the species was abundant everywhere on the tundra edge.

Apparently migrants may arrive at any time of the day or night. I have seen flocks arriving from 0400 to 2330 hours. These flocks are small (10 to 30 individuals; maximum 80) and usually consist entirely of Smith's Longspurs, but sometimes a few Lapland Longspurs (*Calcarius lapponicus*) or Snow Buntings (*Plectrophenax nivalis*) are included.

In most years the males remain in flocks of three to five birds for several days after arriving. Females may join these flocks, but they show no evidence of being attracted by the males and pair formation does not occur until after males become territorial. Lapland Longspurs and Snow Buntings may also associate with the flocks, especially early in the season when the wetter feeding areas preferred by the Laplands are still covered by melt waters. While in flocks the birds spend much time foraging. Walking rapidly over the drier regions of the tundra, they peer and peck under small shrubs and trees; later in the season they often hop or make short flights to catch flying insects. I have never seen a longspur scratch at the substrate.

VOCALIZATIONS

Male Smith's Longspurs, when flocking, sing only sporadically, and then almost invariably from the ground. Their commonest vocalization is a rapid, sharp, rattle, *tic-tic-tic-tic*, that has been aptly likened to the sound of winding a cheap watch (Taverner and Sutton, 1934:31). This call, also given by flying birds, functions as a location note (see below) in keeping the flock together, as an alarm, and as a threat. It is similar to the louder and more musical rattle of the Lapland Longspur. Another note, a short, sneezy *syu*, is sometimes given by flying birds. This call is equivalent to the Lapland's *teu*, but unlike that call, which is given commonly throughout the season and in response to many situations (see Andrew, 1957), the *syu* call is rarely



FIG. 1. Treeline habitat of Smith's Longspur at Churchill, Manitoba. A male is singing from the black spruce in the foreground.

heard. Its major function appears to be as a flocking note in flight, but it is also given by females leaving the nest.

The song of Smith's Longspur is warbler-like and is most reminiscent of those of Yellow or Chestnut-sided warblers. Typically it consists of six to eight

notes, the first several ascending in pitch, the last two descending (sonagram in Borror, 1961:165); the first two notes are delivered at a very low volume and may not be heard except at close range. There is sufficient variation that individual males may be distinguished by their songs. Borror (1961:162) gives a frequency range of 3300 to 6200 cps.

TERRITORIALITY

In this paper I use "territory" loosely to mean the male's activity space at the time of pair formation. Classical territoriality is either ephemeral or lacking in this species, and even with prolonged observation I have been unable to determine what may constitute a "defended area." I consider male Smith's Longspurs territorial when they restrict most of their activities to a specific area and begin to sing persistently from conspicuous, often elevated, sites in response to other males.

In years when the males arrive late the flocks disband almost immediately, but in more normal seasons the transition from flocking to territorial behavior is less sudden. In 1966 males arrived in the first days of June and remained in flocks until 6 June. On that date many males in flocks began to sing frequently from the ground, but the songs were not directed at other males, and they had no noticeable effect on other members of the flock. On 7 June a few males left the flocks briefly and sang from trees, but later rejoined the flocks. By 9 June no flocks persisted and all males were on territory.

Even during the initial stages of the breeding cycle, when in most species territorial behavior is strongest, male Smith's Longspurs show little concern for the physical defense of territory, song perches, nest site, or mate. In claiming a territory they sing once or twice from the top of a small tree, then fly to another; in territories where trees are absent, ridge tops, boulders, or any conspicuous sites are utilized. No regular route through the territory is used, but often they fly to trees that have just been vacated, or to those in which another singing male is present. It is not uncommon to find three males singing from the same tree at the same time without conflict. Unlike other longspurs, Smith's has no flight song, although birds occasionally sing while flying between perches. This behavior is unusual and I did not notice it more frequently in birds whose territories lacked conifers or other conspicuous song perches.

Chasing of other males begins at about the time females arrive on the territories. Yet, even at this time males are not strongly territorial. Not all trespassers are chased. The chases are usually perfunctory and rarely result in fighting; in fact, many end when the males land and begin feeding together. Occasionally Savannah Sparrows and Lapland Longspurs flying through the

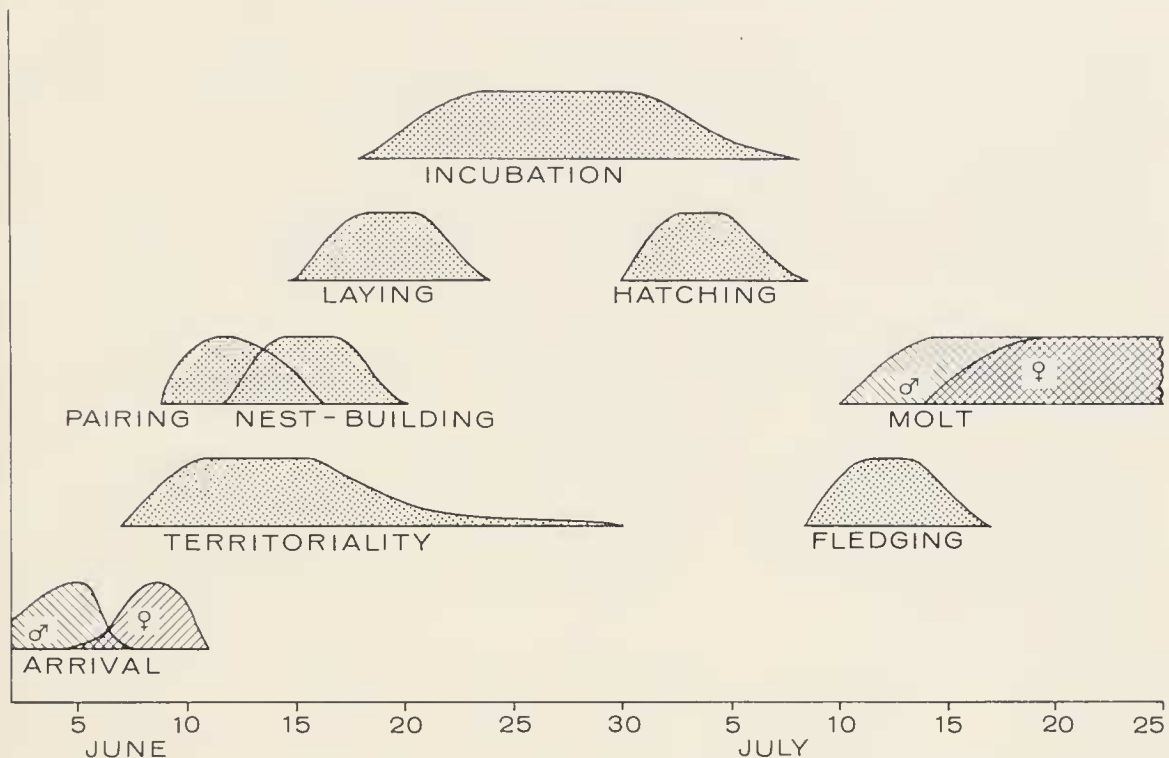


FIG. 2. Summer schedule of Smith's Longspurs at Churchill, Manitoba, in 1966.

territory are pursued, but these chases seem to result from mistaken identity and do not represent occurrences of interspecific territoriality.

By the time females begin building chasing has diminished. At this period males remain near the females in the central part of the territory and rarely wander to the periphery. They continue to sing in response to other males, but the presence of outsiders on the territory provokes no response, as the following observations indicate. On 11 June 1966, a male sang from the top of a small spruce, ten feet away from a potential nest site that his mate had investigated an hour earlier, while another male foraged, and occasionally sang, at the foot of the tree. On 15 June 1966, I watched a pair land 10 feet from a nearly completed nest. The female approached the nest carrying a feather for the lining when a foreign male suddenly flew in and attempted to mount her. A short struggle ensued, after which the female flew away. Her mate, never more than 5 m away, walked around unconcernedly and made no effort to drive off the intruder, which shortly afterwards flew off out of sight.

During the incubation period males again roam through and beyond the entire territory. They may now sing for prolonged periods from one perch, and they still continue to engage their neighbors in brief singing duels, but chasing rarely occurs. Occasionally birds flying over the territory are chased cursorily. Late in the period all semblances of territoriality disappear. Males again join in small flocks and feed together in areas that earlier had contained

only one male. Territoriality does not resume in the nestling period. In 1965, after a severe storm during which most nestlings were killed (Jehl and Hussell, 1966a), I trapped two pairs of adults feeding young at one nest. Presumably the chicks of one pair died during the storm.

Females at no time defend any part of the territory. I have seen them foraging within a few feet of Savannah Sparrows and Lapland Longspurs without incident, and once two females fed within 30 feet of one's nest. Dummies of male Smith's and Lapland longspurs placed at the edge of the nest and enhanced by taped playbacks of Smith's song failed to attract the attention of the males. Females encountering the mounts for the first time stared briefly, then returned to incubating.

Because overt territorial behavior is of such short duration, and because the males' activity space varies at different times of the breeding season, it is difficult to determine territory size. Two territories mapped during the incubation period measured approximately 4.1 and 6.0 acres. In a 50-acre census area four pairs nested in 1965 and 1967, three pairs in 1966. The closest nests were 125 and 158 m apart. The apparent low density is attributable to the interrupted nature of suitable nesting habitat. Nests of Lapland Longspurs and Savannah Sparrows were found within 30 m of Smith's nests and one sparrow nest was less than 10 m distant; in 1965, Hussell found a Lapland Longspur nest 10 m from a Smith's nest.

Return to territory.—Circumstantial evidence suggests that adults return to their breeding areas of previous years.

1. Many males occur in areas that were used in earlier years, and the boundaries of their territories often appear similar to those used previously. For example, in 1967 territorial males occurred in the immediate vicinity of four of the five nests found in 1966. Areas used by three of these males were virtually identical to those of their 1966 counterparts. The fourth male is discussed below (see 4).
2. In 1965, a banded male was seen on the territory of the only adult male Smith's Longspur that I banded in 1964. Since there has been virtually no banding of Smith's Longspurs away from nesting grounds, probably these observations were of the same individual.
3. The area used by pair I-66 was reoccupied in 1967, and the male defended approximately the territory of the 1966 male. The female was first seen on the territory on 11 June and had apparently just arrived. When I investigated the old nest site on that date, as I had done on the previous two days, the female sat on a nearby hummock and rattled at me. This behavior is often encountered in females late in incubation and during the nestling period. I did not find the nest of this pair in 1967, but the female's behavior left no doubt that it was within 100 feet of the 1966 site.

4. In 1965, I collected many nests after the young had perished. Nest 4-66 was found in the same depression as nest E-65; the site, a three-inch depression between two tiny hummocks, is an unusual one for this species. Since the female alone picks the nest site, these observations strongly suggest that this bird returned to her previous nesting area. The territory of the male in this area was virtually identical in 1965 and 1966, which also suggests that some pairs are reformed annually.

I shot the male of this pair after the chicks fledged in 1966. In 1967, I again found a pair in the vicinity, but the territory of the new male was shifted westward and included only about half of the area used by the original male. The female nested within 50 yards of the 1966 nest, within that part of the territory that had also been defended by the previous male. On several occasions she rattled when I approached the vicinity of the original nest.

I have no data on the return of young birds. A few were banded in 1965, but, as noted, nearly all were killed. Seven chicks were banded in 1966; none were found in 1967.

The lack of strongly developed territoriality is one of the most interesting aspects of this species' breeding behavior. One wonders how much of an effect habitat configuration may have on spacing the males, and whether the virtual absence of territorial behavior is in any way related to the physiography. In arctic and subarctic species, breeding time is relatively limited, and long periods spent in territorial defense might be disadvantageous. Re-use of previous territories and their ritualistic defense could reduce intra-specific conflict. On the other hand, Smith's Longspur populations might not attain densities at which competition for nesting space occurs. Thus, selection for active territorial defense may be lacking. Clearly, much additional research is needed to clarify this problem.

NESTING

Pair formation.—As noted, females tend to arrive several days later than males. If they arrive while the males are still flocking, they may join the flocks, but if they arrive later they immediately take up residence on a male's territory. Pairing takes place on the territory and apparently without any conspicuous ground displays such as the wing-up display of McCown's Longspur (DuBois, 1937:235). Often two or three males and one female are observed in rapid, twisting flights over the tundra that extend far beyond the boundaries of any single male, but whether these are pursuit flights associated with courtship or aggressive displays of territorial males toward an already mated pair is not clear.

Nest construction.—Once pairs are formed, the mates are usually encountered together wandering through the territory, maintaining audible

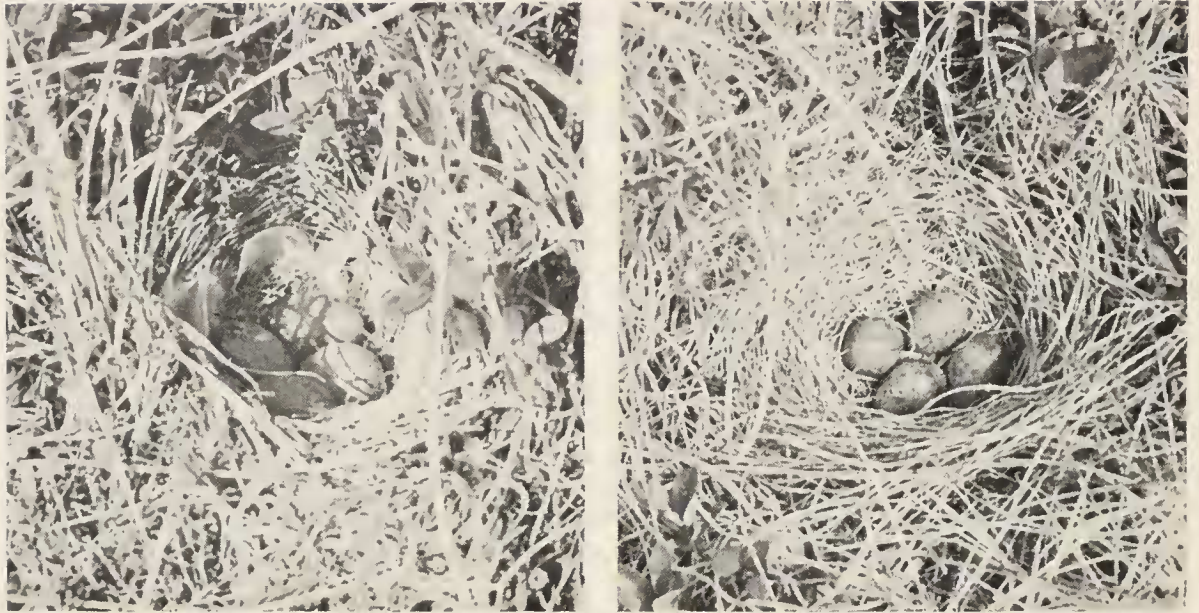


FIG. 3. Left: a typical nest lined with several ptarmigan feathers, among sedges and tiny rhododendrons. Right: an unlined nest concealed among sedges. Note that both nests are unprotected from above.

contact by frequent, single rattles. Several days to a week after pairing the female begins to search for a nest site. She tests the suitability of small depressions by crouching in them and making settling motions. Previous familiarity with an area probably influences the choice of older birds, as noted above. As soon as the site is selected, the female begins to gather nest material. The male takes no part in nest building, although he often accompanies the female to the vicinity of the nest.

Nests are built in three to four days and are made almost entirely of grasslike materials. The outer layer, 8 to 12 mm in thickness, is made of 50 to 85 mm lengths of a coarse, dark brown sedge. The inner layer, 10 to 15 mm thick, is composed of shorter pieces (20 to 60 mm) of a fine, light brown sedge, usually *Scirpus caespitosus*; in some nests a few feathers or tiny scraps of paper are included. The nest cup may be lined with a few feathers; occasionally bits of hair, wool, or reindeer lichen (*Cladonia* spp.) are added (Fig. 3). At 22 nests, the number of feathers in the lining ranged from 0 to 14, with a mean of 3.8. This contrasts strongly with the abundance of feathers found in Lapland Longspur nests. Sandpiper, duck, and Canada Goose (*Branta canadensis*) feathers are sometimes used, but the white breast feathers of winter-plumaged Willow Ptarmigan (*Lagopus lagopus*) are used most commonly, which may merely reflect their greater conspicuousness and abundance rather than color preference by the longspurs. Usually the nest lining is added before or during laying, but one bird added only two feathers after she had begun incubating.

Nest sites.—Unlike nests of Lapland Longspurs at Churchill, which are almost invariably built into the sides of small hummocks and are protected by overhanging vegetation, nests of Smith's Longspurs are commonly unprotected from above, and are built in small depressions atop relatively dry, flat hummocks. Of the thirty nests found, 23 were on ridges: 12 were at the base of a small shrub or tree, 11 were protected only by overhanging sedges. Seven nests were on the sides of hummocks and six of these were concealed by a small shrub or tree, one by sedges; however, not one was as well-protected as most Lapland Longspur nests.

Copulation.—Copulation begins at the start of nest construction and continued at one nest until after the second egg (of four) was laid. It seems to be incited entirely by the female and to occur most frequently after she has added material to the nest. On many occasions I have seen a female fly five to ten feet from the nest, then crouch in a soliciting posture—head back, wings outstretched and vibrating, tail cocked. Twice I have seen behavior that may also be part of a precopulatory display. On these occasions the pair flew off together after the female solicited but failed to entice her mate to mount. On landing both birds leaped a foot into the air and “fought” briefly face-to-face, then dropped to the ground; the female solicited at once, and the male mounted. After copulating the pair may forage together for several minutes. There are no obvious postcopulatory displays.

Laying; eggs.—At two nests for which I have complete data, eggs were laid daily, apparently before 1000 hours, until the clutch was completed. Eggs are pale gray-green with light lavender spots; some are more heavily marked with purplish brown spots or lines, some are almost unmarked. The average dimensions of 16 eggs were 21.6×5.7 mm. Extreme measurements are 23.7×15.5 , 20.2×15.4 , 22.3×15.1 , and 20.5×16.2 .

Incubation.—Incubation is by the female only and at three nests began the night before the final egg was laid. At one of these, an apparently incubating female flushed from the nest the night after her second egg (of four) was laid, but at another the female did not protect her three-egg (of five) clutch on a cold (38 F) and damp night when a heavy mist wet the eggs. The female's attentiveness during incubation seems unrelated to weather conditions. I have twice found nests that were soaked and apparently deserted in which the eggs hatched successfully (see below).

From the start of incubation females sit very closely and do not flush until the observer is quite near. In this respect they differ from Lapland Longspurs at Churchill, which tend to slip away while the observer is still distant. When flushed they fly off a few feet, tail widely spread, and white outer tail feathers conspicuously displayed, then land and crouch with wings slightly drooped, back feathers ruffled, tail spread and flattened on the ground. If pursued,

they alternate short, shuffling runs with brief, low flights until the intruder is led 30 m or more from the nest. Distraction displays I have observed were always silent. If the intruder remains near the nest, however, they return to the vicinity and rattle until he departs. Distraction displays begin at the start of laying.

Departures from undisturbed nests are much different. Females stand briefly at the edge of the nest, then fly off close to the ground giving a rattle that is almost invariably followed by an abbreviated song. One female watched by Hussell occasionally walked away from the nest and fed in the vicinity. Some females sing fully as well as males, whereas others follow the rattle with only a call note, *syu*. Presumably these vocalizations alert males to the females' departure, but I have never seen a male fly toward a departing female, nor have I seen females fly toward the area in which the male was last heard. When off the nest females rattle every few seconds. The bulk of their feeding is done 25 to 50 m from the nest. Except in the early evening, when they may forage with males anywhere on the territory, females rarely go farther than 100 m from their nest. When returning they fly to about 8 m from the nest and walk in, rattling every few seconds until within 2 m of the nest; this distance is covered silently. After the characteristic departing and returning behavior is recognized nests can be easily located. Hussell observed one female that gave a "quiet and short murmuring note . . . *kwer-kwer-kwer-kwer*" when settling on the eggs.

The constancy of incubation seems to increase as the incubation period progresses. On the sixth day of incubation between 16:10 and 18:14 hours one female spent 55 minutes on and 41 minutes off the nest; attentive periods averaged 11 minutes (range 8 to 14 minutes), inattentive periods 10 minutes (range 7 to 17). In the midafternoon of the tenth and eleventh days of incubation I watched her for 63 and 56 minutes, respectively; on both days she left the nest only once, to defecate, and returned within one minute. Air temperatures were in the upper 60's on all three days and the female panted continuously while incubating.

Males rarely approach the nest, though they may land nearby and rattle when humans are in the vicinity. The alarm calls of females are usually ignored. Male McCown's Longspurs feed incubating females (DuBois, 1927), but male Smith's apparently do not. I once saw a male land within five feet of an incubating female who immediately began begging, but the male, whose bill was empty, merely paused for a moment and then flew off. Possibly my presence in the blind affected his behavior.

Incubation period.—Jehl and Hussell (1966*b*) reported periods of 11½ to 12 days for eggs incubated during favorable weather in 1965. In addition, a period of 13 days, 12 hours (± 6 hours) in 1966 and a period of at least 13



FIG. 4. Male Smith's Longspur feeding nestlings approximately two days old. The male has already molted the inner primaries.

days, 20 hours in 1967 were determined. All periods were calculated from the time of laying to hatching of the last egg. In both of the latter years inclement weather occurred during incubation and the eggs at both nests were found cold, wet, and apparently deserted, after four and six days of incubation, respectively. It seems probable that chilling delayed normal development.

At eight nests the time required for the hatching of the entire clutch ranged from a maximum of 11 to 36 hours, with a mean of approximately 22 hours. Eggs hatch within a day after the first signs of cracking appear, and often only a few hours are required.

In general, the hatching period for the Churchill population occupies only a few days. In 1965 eggs hatched from 3 to 13 July, but at 17 of 21 nests the hatch occurred between 3 and 6 July. At the five nests that I studied in 1966 the chicks hatched between 1 and 4 July, although subsequent observations showed that a few other nests hatched later. In 1967 hatching dates from 6 to 10 July were recorded; later hatchings were probable.

THE NESTLING PERIOD

For about two days after hatching chicks are fed largely by the female. Caterpillars, grasshoppers, and adult Diptera and Lepidoptera are the most conspicuous foods carried in by the adults, but many other foods are utilized



FIG. 5. Female "airing the bed" at a nest at the base of a dwarf birch.

(see below). Nestlings receive their first feeding within a few hours of hatching; this accounts for the great variation in weights of newly-hatched (D-0) young (Table 2).

The male's role in feeding the nestlings increases gradually and by D-2 or D-3 equals that of the female. In the first days after hatching he forages widely over the territory and feeds the chicks (Fig. 4) at irregular intervals. As his attentiveness increases, his foraging area becomes reduced. Females rarely forage more than 50 m from the nest.

When approaching the nest with food, both parents give a short rattle, upon which the other parent leaves the vicinity of the nest. Fecal sacs are removed by both parents: usually the first sac is eaten, but if the nest contains two or more the additional sacs are carried off. Egg shells and dead chicks also disappear from the nest, and presumably are removed by the adults.

I never encountered males brooding the young, but once on a warm afternoon I watched a male shade the nestlings for approximately one minute. He left before the female returned to the nest. At one nest Hussell reported that the male brooded 2½ to 3-day-old chicks for 5 and 8 minutes after feeding them. After feeding the chicks the female broods them for a few minutes, even on the warmest days. While brooding she may peer into the nest, then probe

TABLE 1

OBSERVATIONS ON THE GROWTH AND DEVELOPMENT OF SMITH'S LONGSPUR NESTLINGS

Day 0	Skin pale orange (bright orange for a few hours after hatching: D. J. T. Hussell), mouth lining pale pink; eyes closed. Down buffy (closest to Cartridge Buff of Ridgway, 1912), 10-12 mm long, tipped with dusky gray, thick on capital, humeral, and dorsal region of spinal tract, sparse on femoral tracts; papillae in cervical region noticeable by 4 hours after hatching. Chicks placed on back roll over only with great difficulty.
Day 1	No obvious change in distribution of down; papillae in cervical region dark and prominent. Able to balance and gape. Beg in response to female's rattle.
Day 2	Feather tracts appear all over body (in some birds by D 1½), papillae of primaries visible, but less than 1 mm. Chicks sit up and gape when nest is vibrated. Uric acid adheres to chicks.
Day 3	Feather sheaths conspicuous on crown, neck, scapulars, wings, flanks, less developed on venter. Eyes begin to open on largest chicks; faint, high-pitched begging squeaks. Mouth lining reddish. Fecal sacs deposited.
Day 4	Feathers start to break from sheaths on venter, flanks, a few on back; minor wing feathers well-defined. Eyes open. Begging louder, audible 10 feet from nest. Will gape to visual stimulus as well as sound (Hussell).
Day 5	Like D-4 but feathers longer, many more breaking from sheaths; head feathers nearly free of sheaths.
Day 6	Chicks appear fully feathered dorsally, though tailless; primaries and coverts breaking from sheaths, other wing feathers more advanced. High-pitched begging can be heard 20 feet away. Egg tooth still retained (in some chicks) (Fig. 6).
Day 7	Like D-6 but larger. Primaries free for 3-4 mm, secondaries and coverts almost free of sheaths. Much of venter feathers covered. Largest chicks leave nest. Chicks homeothermal.
Day 8	Larger, belly completely covered by feathers. Nearly all traces of down lost.
Day 9-12	Growing rapidly. D-11, down has disappeared. D-12, wing now a solid flying surface; chicks able to fly a few inches after short runs. Tail 8 mm. Egg tooth visible in some chicks.
Day 13	Able to fly over 18" wire fence.

vigorously at the lining for a few seconds (Fig. 5). One female repeated this performance six times in the span of a few minutes. I have seen this behavior, which has been called "airing the bed," between D-2 and D-7. Royama (1966:320) believes that its major function is insulative. Of course, rearrangement of a matted nest lining will necessarily aid in heat retention, but I question whether this is the function of the behavior, for I have seen it done by panting females on warm days when the need for increased insulation seems negligible. Whenever I have observed the behavior it has occurred *after* the female has resumed brooding. The probing appears to be directed at one specific area of the nest, not the entire nest lining. During my brief



FIG. 6. A six-day-old Smith's Longspur nestling.

observations the female probed vertically, never at the sides of the nest cup. From these observations I infer that "airing the bed" is primarily a comfort movement. Perhaps the chicks' movements cause small bits of the nest lining to protrude and irritate the brood patch. Hussell (pers. comm.) observed "airing the bed" behavior from an *incubating* female, who removed "a piece of fine grass about 1½" long . . . and flew away with it." More detailed observations of this behavior, including precise observations on the areas probed, are needed. An experimental approach (artificially tamping the nest lining, inserting stiff bits of grass into the nest lining, etc.) might be used profitably.

Chicks begin to stray short distances from the nest by D-6, but they do not desert it until D-7 or, less frequently, D-8. At this time they are able to run fairly rapidly through the grass, but when approached they crouch motionless under small shrubs. By D-12 the chicks can fly short distances, but several more days are required before they can fly well. Whether the parents play any part in leading the chicks from the nest is unstudied, but I suspect that at least the chicks' initial movements are unguided.

Growth and development of the young.—Observations on the growth and development of nestlings are summarized in Table 1. In Tables 2 and 3, growth

TABLE 2
DAILY WEIGHTS AND PER CENT RELATIVE GROWTH RATES OF SMITH'S AND
LAPLAND LONGSPURS

Age in days	Number of chicks	Smith's Longspur ^a				Lapland Longspur ^b		
		Weight: range and mean, g		Mean weight change, g	Per cent relative growth/day	Mean weight, g	Mean weight change, g	Per cent relative growth/day
0	9	1.6-3.0	2.6			2.3		
1	9	3.8-4.9	4.5	1.9	53.4	3.5	1.2	41.9
2	9	6.2-7.8	7.1	2.6	44.8	5.2	1.7	39.6
3	9	8.4-12.5	10.7	3.6	40.4	8.0	2.8	43.0
4	9	8.7-16.0	12.8	2.1	17.6	10.6	2.6	28.1
5	9	9.3-20.2	15.9	3.1	21.6	14.0	3.4	27.8
6	9	11.0-22.4	18.3	2.4	14.0	17.2	3.2	20.5
7	2	21.9, 22.0	22.0	3.7	18.3	18.8	1.6	9.0
8	1 ^c		20.3			19.9		
9	1 ^c		16.1			21.2		
10	1 ^c		18.6			21.3		
11	1 ^c		20.5			22.4		
12	1 ^c		22.0			21.9		

^a Data for successfully fledging chicks.

^b Data from Maher, 1964, Table 2.

^c Bird retained in wire enclosure at nest.

rates, as indicated by daily weight changes and by the growth of the seventh (i.e., third outermost) primary, are compared with those of Lapland Longspurs (data from Maher, 1964). For individual recognition I dyed chicks lightly on the wing or thigh with Magic Marker until they were large enough to band.

I visited nests daily about midday during the hatching period and noted the condition of the eggs. From this, and from later observations on the size and condition of the young, the approximate hatching time could be established. In this study chicks assigned to D-0 averaged 12 hours old (range 0 to 18), D-1 chicks 36 hours (range 18 to 42). According to D. J. T. Hussell (pers. comm.), Maher's D-0 chicks averaged about 6 hours old, D-1 chicks 24 hours. Thus the more rapid growth of Smith's nestlings indicated in the tables probably stems largely from differences in the average age of chicks in each category. My small sample and my restriction of data to chicks fledged successfully tend to accentuate the differences. I doubt that there are any important differences between these species in growth rate and development.

In 1966, I made brief observations on the thermoregulatory ability of nestlings. Immediately on arriving at a nest, I recorded the chicks' cloacal temperatures to the nearest 0.1 C with a Wesco fast-recording thermometer

TABLE 3
GROWTH OF THE SEVENTH PRIMARY IN SMITH'S AND LAPLAND LONGSPURS

Age in days	Smith's Longspur ^a		Lapland Longspur ^b	
	Number of chicks	Range and mean in mm		Mean
2	7	0-1.0	0.5 (est.)	0.02
3	7	1.0-2.5	1.9	0.9
4	7	2.8-4.9	3.9	2.3
5	7	5.5-9.2	7.3	5.8
6	7	9.5-13.4	11.5	10.3
7	2	14.8, 20.0	17.4	14.3
8	1 ^c		23.5	19.9
9	1 ^c		27.0	24.1
10	1 ^c		31.5	30.0
11	1 ^c		35.0	34.3
12	1 ^c		38.0	37.9

^a Data for successfully fledging chicks.

^b Data from Maher, 1964, Table 3.

^c Bird retained in wire enclosure at nest.

inserted to a depth of 12 mm. Chicks were then placed singly in shaded, wind-free areas (usually in my hat and under a small shrub) for ten minutes, after which time their cloacal temperatures and the ambient temperature in the shaded region were recorded. Some representative observations are given in Table 4.

The development of homeothermy was clearly correlated with the growth of the feathers. Pin-feathered chicks three and four days old were unable to maintain their body temperatures under the test conditions for even a few minutes. Improved thermoregulatory ability is evident by D-6, when most feathers of the dorsum have broken free of their sheaths. By D-7, when much of the ventral apertium becomes covered by feathers, chicks are able to maintain their body temperatures for prolonged periods. Maher (1964) found that Lapland Longspur and Snow Bunting chicks were able to maintain their body temperatures at low ambient temperatures by D-7, but that their ability to reduce body temperatures at high environmental temperatures began several days earlier.

DISPERSAL AND DEPARTURE

Disruption of family groups begins shortly after the chicks leave the nest. I have found nestmates 40 m from each other one day after fledging, and several days later the family may be scattered over a quarter-mile of tundra. The parents maintain audible contact for a few days, but within a week after the chicks fledge calling between the adults has virtually ceased, and most

TABLE 4
THERMOREGULATION IN SMITH'S LONGSPUR NESTLINGS

Chick number	Age in days	Cloacal temperature, C	Cloacal temperature 10 minutes after chick removed from nest, C	Ambient temperature, C
4-1-66	3	35.4	24.6 ^a	12.0
2-2-66	4	31.5	26.0 ^a	13.2
1-3-66	5	35.8	30.0	24.8
1-4-66	5	36.0	31.0	24.8
3-1-66	5	40.4	36.5	not recorded ^b
3-1-66	6	39.1	37.1	21.5
4-2-66	6	39.8	37.6	21.5
3-1-66	7	36.4	37.5 ^c	17.0

^a Body temperature recorded after five minutes.

^b Ground temperature at nest 40.2 C; chick panting vigorously.

^c After 1½ hours at 27 C, chick's body temperature was 39.5 C.

chicks encountered are accompanied by only one adult. It appears that each chick, from the time it leaves the nest, is fed by only one of the parents. This enhances rapid dispersal and disruption of the family into two groups. As Maher (1964) pointed out, early fledging and dispersal of ground-nesting passerines is important in reducing losses to predators.

The male's former territorial boundaries have no significance after the chicks leave the nest. Some family groups rapidly disappear from the territory, whereas others remain on it, independently, for prolonged periods. I have found banded D-22 chicks in association with the male parent, within 100 m of the nest site.

Distraction displays by the parents usually cease when the young are able to fly, or at about D-13, but I have seen one from a female with D-20 chicks. However, adults usually respond to humans near their chicks by rattling vigorously from the tops of small trees, while the chicks fly off a short distance.

The chicks are fed for about three weeks after hatching, but in late July the adults leave them and gather in small flocks. Migration begins as early as mid-August in some years (Taverner and Sutton, 1934:80) and by early September all Smith's Longspurs have left the Churchill region. The possibility of differential migration of age and sex classes might be profitably investigated in this species, because of the earlier incidence of the males' postbreeding molt (see below).

PRODUCTIVITY

Clutch size and hatching success data for 1965-1967 are given in Table 5. The median clutch was four and clutches of two to five were found, but the

TABLE 5
CLUTCH SIZE AND HATCHING SUCCESS OF SMITH'S LONGSPURS AT CHURCHILL, MANITOBA,
1965-1967

Year	Clutch size					Hatching success by year
	2	3	4	5	\bar{X}	
1965		2	16	3	4.05	81/85 (95.4%)
1966	1*		4		3.60	16/18 (88.8%)
1967		1	3		3.75	10/11 (90.1%)
Total	1	3	23	3	3.93	107/114(93.7%)
Hatching success by clutch size	1/2 (50%)	8/9 (88.8%)	84/88 (95.4%)	14/15 (93.3%)		

* See text for explanation.

single two-egg clutch is suspect. It was discovered late in the incubation period, one egg disappeared just prior to hatching, and the nestling was killed by a weasel (probably *Mustela erminea*). Possibly this predator removed some eggs on earlier visits. Pough (1946:275), without stated authority, reported clutches of four to six.

Hatching success was consistently high. Only seven of 114 eggs failed to hatch; three disappeared from the nest, two were infertile (egg broken, no embryo present), one was apparently infertile (not examined), and one pipped egg failed to hatch.

Fledging success was poor in 1965. All nestlings in 18 nests under observation on 8 July died from exposure (Jehl and Hussell, 1966a) and probably less than five per cent of the eggs produced fledged young. In 1966, 16 of 18 eggs hatched, but only 9 young left the nest. One chick was killed by a weasel. The growth rate of three chicks in nest 1 declined on D-3 and by D-5 two had died. It is difficult to explain this loss, but the male only rarely fed the nestlings, and I suspect that the female alone was unequal to the task. Four chicks in nest 2 grew rapidly through D-3, but on D-4 I found them cold, damp, and begging for food; two days later all were dead, apparently from exposure. At both of these nests at least one parent fed the chicks after they were weighed, so it seems unlikely that nestling loss was attributable to my activities. I have no data for 1967. At the time of my departure there had been no loss of nestlings, and chicks in all nests were growing normally.

In most years productivity should be high. The only potential mammalian predators on eggs or young are weasels, red foxes (*Vulpes fulva*), collared lemmings (*Dicrostonyx groenlandicus*) and voles (*Microtus spp.*): the first two are extremely rare and I have no evidence that the rodents prey on eggs, even in years when their populations are high. Common Ravens (*Corvus*

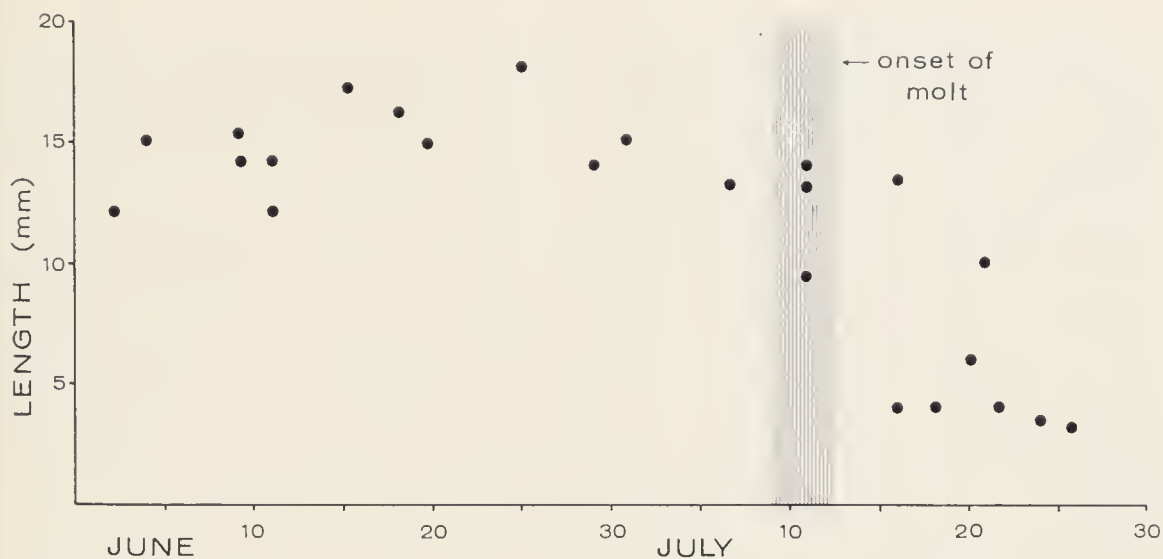


FIG. 7. Seasonal change in testes length of Smith's Longspurs.

corax), Short-eared Owls (*Asio flammeus*), gulls (mainly *Larus argentatus* and *L. thayeri*), and occasionally Parasitic Jaegers (*Stercorarius parasiticus*) may take a few chicks, but their effects seem negligible. In fact, longspurs show no concern about the occurrence of avian predators near their nests. The most important factor limiting productivity in the period of my studies was adverse weather (see Jehl and Hussell, 1966a).

I have no evidence of re-nesting, which indirectly suggests little nest predation. Judged by testes size (Fig. 7), the males remain sexually active into early July and thus re-nesting could be attempted if the eggs were destroyed. However, re-nesting did not follow the loss of nestlings in 1965, presumably because testicular regression had begun by this stage of the breeding cycle.

MOLT

Postbreeding molt.—The incidence of the postbreeding molt may be photoperiodically controlled in part, for each year males began molting on approximately 10 July. At this time in 1966 some chicks had already left the nest, whereas in 1967 the nestling period was hardly started. Females start molting four or five days later than males. The innermost primary and its covert are the first feathers lost; a few birds molt primaries 1 and 2 concurrently. The remaining primaries are shed in ascending order, the interval between the loss of adjacent primaries being three or four days. Molt on the upper chest, flanks, and thighs follows, and becomes conspicuous at about the time primary 4 is lost; some birds molt the distal tertial and its covert at this time.

The start of the secondary molt approximately coincides with the loss of

primary 7. By this time extensive molt is visible everywhere on the body and the innermost primaries are nearly regrown. The underwing coverts and most of the smaller upper wing coverts seem to be molted after most of the primaries are shed. The replacement of a primary requires about 12 days; one captive bird replaced a secondary in 10 days.

The tail is lost as a unit in late July or early August, or at about the time primary 8 is lost, and its replacement is completed before that of the innermost secondaries. Of three birds collected at Churchill on 25 and 26 August 1936, one had a fully grown tail, those of the others being about 90 per cent grown. These birds had completed body molt, but their outermost primary was only three-quarters grown. Since Smith's Longspurs leave Churchill in late August, many must migrate before finishing the molt.

Young birds begin the postjuvinal molt at about 20 days of age. Presumably this molt involves only the body feathers. I have no data on its duration but, as with the adults, it must often be completed south of the breeding grounds.

Prebreeding molt.—The breeding plumage is attained through an extensive molt that involves all the feathers of the head and body and some, though probably not all, of the smaller wing coverts. The rectrices and the remiges and their major coverts are not replaced. In Lapland (*Calcarius lapponicus*) and Chestnut-collared (*C. ornatus*), and probably McCown's (*C. mccownii*)² longspurs, the breeding plumage is attained largely through wear. Both Lapland and Chestnut-collared longspurs molt some head feathers (Dwight, 1900) and a male Lapland Longspur that I kept in captivity also replaced the scapulars and a few feathers on the thigh and upper back. The significance of the more extensive molt in Smith's Longspur remains to be determined.

In captive birds molt first occurred on the insides of the legs and in the interscapular region, and was followed shortly by the loss of a few feathers from the upper part of the chest. Molt of both the dorsal and ventral tracts proceeded gradually tailward, but extensive molt of the ventral tract did not begin until that of the anterior half of the dorsal tract was well advanced. Feathers of the neck, throat, abdomen, flanks, and the tail coverts were replaced next, and finally, the head feathers and some of the wing coverts were molted.

In 1966 and 1967 captives began molting between 20 and 25 March and had virtually completed the molt by late April. It seems probable that this period corresponds to that of wild birds, for Kemsies and Austing (1950:37) reported that four males collected in Ohio on 18 April 1919 were "nearly in full breeding plumage."

²I follow Sibley and Pettingill (1955) in treating *Rhynchophanes* as a synonym of *Calcarius*.

FOOD

Stomach contents of 39 adults and two flying juveniles collected between 2 June and 26 July were examined. For convenience in analysis, the sample was arbitrarily subdivided as follows: 2-9 June (7 stomachs); 13-18 June (5); 25-30 June (3); 1-9 July (4); 11-20 July (14); 21-26 July (8, including 2 juveniles). Because of fragmentation and decomposition, invertebrates encountered were rarely identifiable to family level, which precluded accurate quantitative or volumetric analysis. However, it is clear that Smith's Longspurs feed opportunistically on a wide variety of organisms through much of the summer. In the first ten days of June, plant materials, principally seeds, make up over 90 per cent by volume of the total food intake; invertebrates are taken when available, adults of terrestrial forms (ants, spiders, beetles) and larval Lepidoptera occurring with greatest frequency. In mid-June, as invertebrates become commoner, the birds switch to a largely animal diet; flying insects begin to be encountered at this time. After 20 June or so, more than 85 per cent of the diet is animal matter, of which the bulk is terrestrial forms or immature stages of flying insects.

Few seasonal differences in foods taken could be determined from this small sample. Seeds which compose the bulk of the diet before 10 June constituted an almost negligible portion thereafter. Ants and spiders were also taken frequently in early June, but none were found in July-taken adults; apparently they are ignored as larger invertebrates become more conspicuous. Snails were found in five of 14 birds taken between 11 and 20 July. Their occurrence reflects the drying of small tundra pools, and there is no reason to suggest that they were taken in lieu of grit. From late June through July adults of flying insects appeared to make up less than 25 per cent of the diet. I would expect them to occur with increasing frequency in August, and for seeds again to compose an important part of the diet later in the month. Grit, largely the easily identifiable local limestone, was found in all but three stomachs.

Nestlings.—The stomachs of 29 nestlings killed during the severe storm of 8 July 1965 (see Jehl and Hussell, 1966a) were also examined. These were grouped for analysis according to the weight of the chicks: 1.6 to 2.8 g (8 stomachs), 3.2 to 3.6 g (7), 4.1 to 5.2 g (8), and 7.1 to 14.7 g (6); these categories roughly correspond to D-0, D-1, D-1 to D-2, and D-2 and older chicks. I found no differences in foods present among these groups and, as with the adults, no specific foods were found in quantity.

With one exception—the occurrence of spiders in 7 of 29 nestlings, but in none of the adults collected after late June—I detected no differences between food received by the chicks and that taken by the adults between 1-20 July

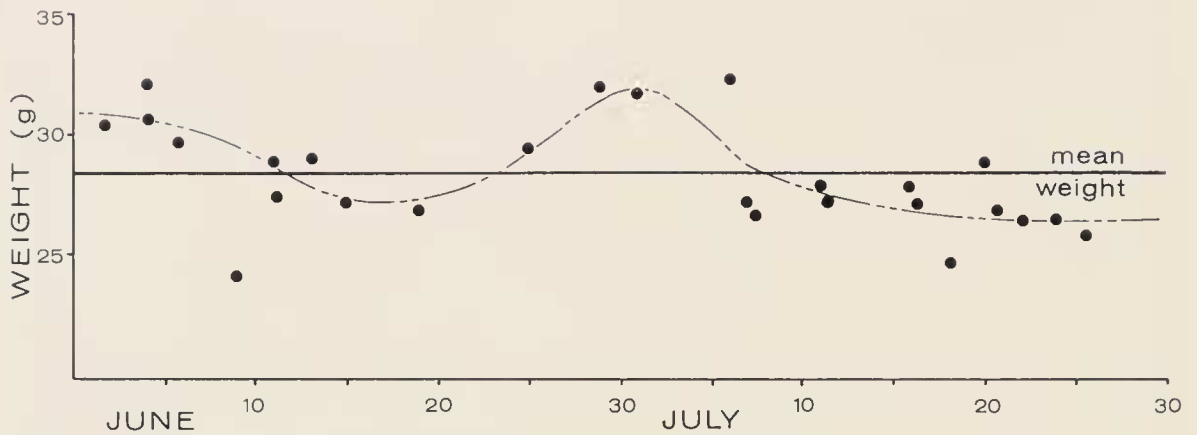


FIG. 8. Seasonal weight changes in male Smith's Longspurs.

(the 1–10 July sample was too small for comparison). Whether or not this difference is significant cannot be determined. I must emphasize that data from the nestlings are potentially strongly biased, since poor weather may have prevented the adults from gathering foods that normally would have been passed on to the chicks.

Entire leaves of plants commonly occurring in the nesting area were found in the stomachs of five nestlings but in none of the adults. They are ingested, as I have observed many times in the field, after accidentally adhering to the chicks' mouth lining. Grit occurred in trace quantities in three of 14 nestlings judged to be D-1 or less, but in large quantities in 11 of the older chicks. Since nests are not placed in gravelly areas, grit cannot be taken accidentally and it must be acquired from the parents.

Foods identified in the stomachs of adults and nestlings are listed below. Unless otherwise noted, all identifications pertain to adult organisms. Arachnida: Areneida. Odonata: Zygoptera. Orthoptera: Acrididae (adults and immatures), Locustidae. Dermaptera: unassigned adult. Hemiptera: Circadellidae. Lepidoptera: Geometridae? (larvae), Noctuidae, unassigned larvae and pupae. Diptera: Tipulidae, Anthomiidae (larva), unassigned larvae, pupae, adults. Coleoptera: Cantharidae, Chrysomelidae (larva), unassigned adults. Hymenoptera: Formicidae, Pompilidae?, unassigned adults. Mollusca: *Stagnicola* sp., *Gyraulus* sp. Plant Material: seeds (including *Potentilla*?), leaves (*Salix reticulata*, *Dryas integrifolia*, *Arctostaphylos* sp.), other (stem fragments, *Cladonia* sp.).

WEIGHTS

Seasonal weight changes in male Smith's Longspurs are plotted in Figure 8. Data for 1966 and 1967 are included, but because breeding began later in 1967 the data for that year are adjusted to the 1966 schedule by plotting them

five days early. The changes are not random but vary predictably with respect to the birds' activities (see Fig. 2). Males arriving on the breeding grounds retain small amounts of subcutaneous fat and are relatively heavy. Their weight declines coincident with the start of territorial behavior, increases late in the incubation period after territoriality has ceased, and declines again in early July, when the males begin feeding the nestlings and molting. I have insufficient data to determine whether seasonal weight changes also occur in females.

The mean weight of 26 males was 28.1 g (range 24.1–31.1), that of 11 females 25.9 g (range 23.8–28.9).

RELATIONSHIPS OF SMITH'S LONGSPUR

The genus *Calcarius* comprises four species, of which three are Nearctic: Smith's Longspur is a subarctic, treeline form; Chestnut-collared and McCown's longspurs inhabit the plains of the western United States and southern Canada; the Lapland Longspur is a Holarctic, tundra-breeding species. Since relationships within this genus are unstudied, I had hoped that this investigation might clarify whether Smith's Longspur was more closely related to the tundra or prairie species. Unfortunately, there is insufficient evidence to resolve this point. Since Smith's lacks some attributes of Laplands that are usually associated with arctic birds, derivation from a tundra-adapted ancestor cannot be strongly contended. For example, Smith's Longspurs nest in exposed situations, Laplands in more sheltered spots. Smith's nests, unlike those of Laplands, are never heavily insulated with feathers; the average clutch size of Smith's (3.93 for 30 nests) is smaller than that of Laplands, even of the southern, Churchill population (4.48 for 19 nests). In these respects Smith's is more like the prairie species (nests unprotected and rarely insulated; clutch sizes relatively small: *mccownii*, 3.58 for 52 nests; *ornatus*, 4.24 for 21 nests; DuBois, 1935), but these are inadequate reasons for suggesting relationship to those species. Smith's Longspurs' early postbreeding molt is an apparent adaptation to high latitudes; however, the molt of other longspurs has not been studied in detail, so the significance of this character is unknown.

There is, in fact, little to indicate that Smith's Longspur is closely related to any modern species of *Calcarius*. Its plumage color and pattern are unlike those of other longspurs, and its simple, warbler-like song is quite different from that of *lapponicus* or *ornatus* (see sonagrams in Borror, 1961:165, 169; Robbins et al., 1966:324) and presumably, *mccownii* (description in Peterson, 1947:239; Borror, 1961:173). Furthermore, unlike the other species, *pictus* lacks a flight song.

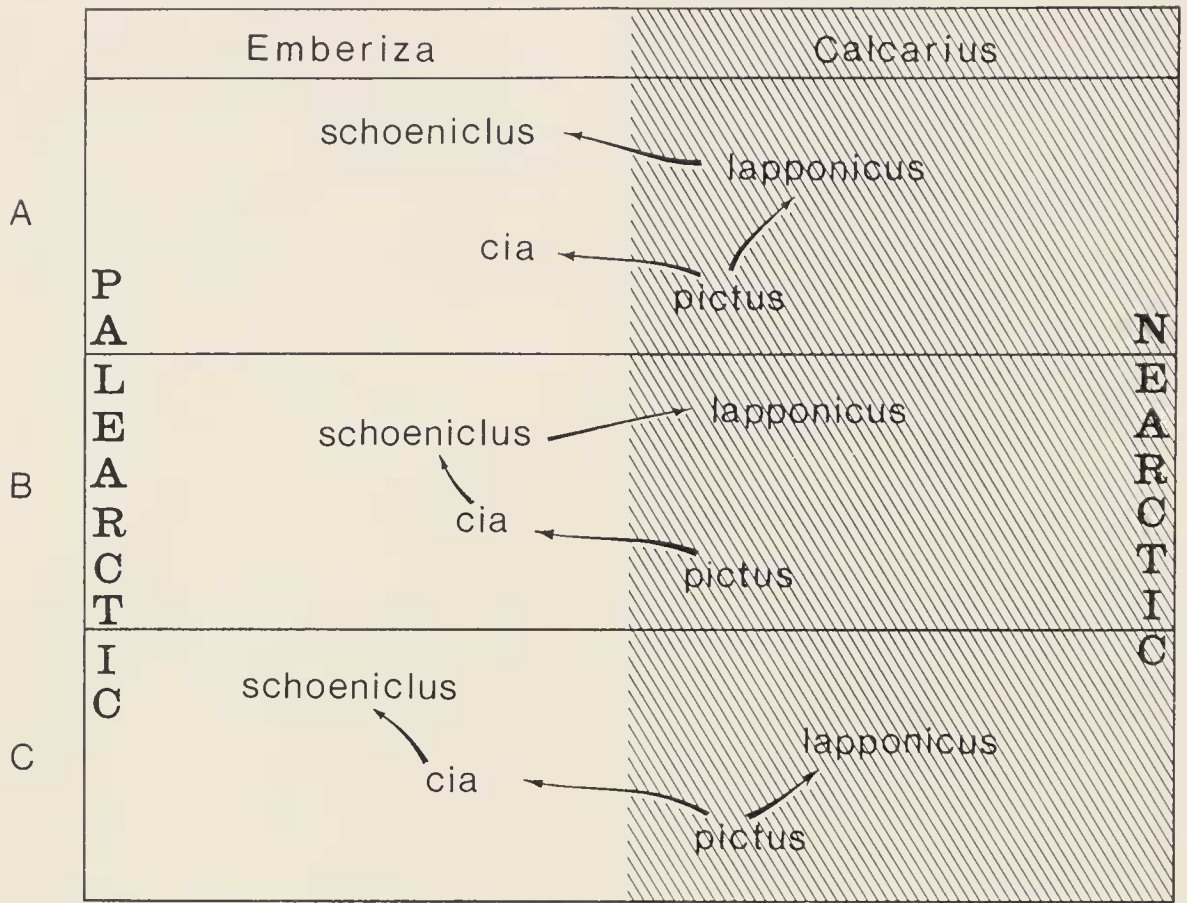


FIG. 9. Some possible relationships between longspurs (*Calcarius*) and Old World buntings (*Emberiza*).

It may be unwise, however, to speculate on longspur interrelationships without also considering the Old World buntings. It is generally acknowledged that *Calcarius* is most closely allied to the Old World genus *Emberiza*. Harrison (1967:26) recently suggested that "the Old World buntings in their evolution from the New World sparrow stock have passed through a phase similar to that shown by the longspurs, or share a common ancestry with them . . . Such a derivation would be a reasonable conclusion since the spread of Nearctic Embrizidae into Eurasia would be most likely to have occurred via a northern land-bridge or short sea crossing and would have occurred most easily if the invading stock was adapted to tundra-like conditions . . . The notion of a common ancestry of longspurs and Old World buntings could be further argued with reference to the close similarity between the Lapland Longspur [*C. lapponicus*] and the present Eurasian longspur [= *C. lapponicus* subsp.?], and the buntings of the Little Bunting (*E. pusilla*)-Reed Bunting (*E. schoeniclus*)-Rustic Bunting (*E. rustica*) subgroup."

This suggestion is reasonable. However, plumage similarities between Lapland Longspurs and Reed Buntings are comparable to those between

Smith's Longspurs and Rock Buntings (*E. cia*). Thus, by similar reasoning, a *pictus*-like ancestor for *Emberiza* can be postulated. Harrison's theory that *Emberiza* was derived from a "tundra-adapted" species seems to gain support from the fact that *Emberiza* includes forms similar to *pictus* and *lapponicus*, but not to either of the plains longspurs.

Ramifications of Harrison's view on the origin of *Emberiza*, diagrammed in Figure 9, seem pertinent to understanding relationships within *Calcarius*. For simplicity, I have arbitrarily assumed that Smith's Longspur is most like the stock from which *Emberiza* was derived. In Figure 9A, for example, postulated that a *pictus*-like ancestor gave rise to "*lapponicus*" and that each of these gave rise to different species groups now placed in *Emberiza*. By this scheme, *Emberiza* is polyphyletic. In Figure 9B, "*pictus*" is postulated to have given rise to the "*cia*" group of *Emberiza*, from which the "*schoeniclus*" group was derived, and which, in turn, gave rise to another "longspur," *lapponicus*. This view regards *Calcarius* as polyphyletic. In Figure 9C, it is assumed that "*pictus*" gave rise to "*lapponicus*" as well as to the "*cia*" group, and that the *schoeniclus* group was derived from the latter. This scheme retains monophyly for both genera, but it raises the problem of explaining the parallel evolution of similar plumages in *Emberiza* and *Calcarius*. (Note that these diagrams may be read in reverse, by assuming that "*lapponicus*" is more like the ancestral stock; however, this in no way relieves the taxonomic dilemmas.) Each of these speculations is consistent with Harrison's thesis, but none is currently testable. Hopefully, as further information on the biology of other species of *Calcarius* and *Emberiza* becomes available, the evolutionary relationships within and between these genera will be clarified. Data on vocalizations of species in the "*cia*" group of *Emberiza*, on the timing of the molts and the extent of the prebreeding molt in *Emberiza* and the other species of *Calcarius*, and on the presence or absence of a flight song in *Emberiza* species may prove to be of greatest importance.

SUMMARY

Observations on the summer biology of Smith's Longspur (*Calcarius pictus*), a subarctic species that nests along the treeline from Ontario to Alaska, were made at Churchill, Manitoba, in the summers of 1964, 1965, 1966, and 1967. Males arrive at Churchill in small flocks in late May or early June, the females a few days later. Several days after arriving flocks break up and males begin to claim territories. There is evidence that some birds re-use territories in subsequent years. Territoriality is not strongly developed in this species, and males make little attempt to defend their activity space, song perches, mate, or nest site. By a week after pair formation, which takes place on the territory and without any conspicuous displays, territorial behavior virtually disappears.

Nests are built entirely by the female, usually in small depressions atop relatively flat, dry hummocks; they are lined with few feathers. Eggs are laid daily, the mean is

four. Only females incubate. Incubation periods of 11½ to at least 13 days 20 hours have been recorded.

For about two days after hatching, chicks are fed mainly by the female; by D-2 or D-3 the male's role equals that of the female. Detailed notes on the growth and development of the nestlings are included. The chicks become homeothermal by D-7, when they begin to leave the nest; they are able to fly short distances by D-13.

After leaving the nest, chicks are fed mainly by only one of the parents, which hastens the disruption of the family. When the chicks are about three weeks old, the parents desert them and form small flocks. Smith's Longspurs leave the Churchill area by early September.

Hatching success was consistently high during this study, and only 7 of 114 eggs failed to hatch. Fledging success was 50 per cent in 1966, but less than 5 per cent in 1965. In 1965 most nestlings died of exposure during a severe storm. Adverse weather was the most important factor limiting productivity in the period of this study.

The timing and extent of the postbreeding and prebreeding molts are described. The postbreeding molt begins in early July and may not be completed before the birds migrate. Males start molting a few days earlier than females.

Stomach contents of 70 birds, including 29 nestlings, were examined. In early June the adults feed mainly on seeds, but from mid-June through July animal matter, mainly terrestrial insects and larval stages of flying insects, composed the bulk of the diet. Seasonal weight changes in males are correlated with changes in activity.

The relationships of Smith's Longspur are not yet clear. It would appear that interrelationships in *Calcarius* may not be resolvable without also considering the relationship between *Calcarius* and *Emberiza*.

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